POST-ERUPTION SUCCESSION ON ISLA FERNANDINA, GALÁPAGOS

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Abstract

In 1968 the mixed shrub forest on the western caldera rim of Isla Fernandina, Galápagos, was buried by a major eruption of tephra. In June, 1971; July, 1973; and August, 1977, vegetation on the western rim was quantitatively sampled in plots along a transect extending 1.5 km from deep, barren tephra to the undestroyed original vegetation. In the 9 years following the eruption, only a few species of weedy composites and grasses became sparsely established in gullies on the deep tephra. By contrast, where the original plants were shallowly buried, vigorous vegetative sprouting of shrubs and of rhizomatous perennial herbs resulted in nearly complete cover by 1977. Species apparently reproducing only by seed returned more slowly than those species with vegetative reproduction. Land iguana activity and precipitation appear to influence the rate and patterns of revegetation. The shrub forest is composed of weedy species able to survive volcanic disturbance and revegetate newly created open habitats.

Rarely is the opportunity available to begin a study of plant succession immediately following volcanic activity. The studies that have been done were usually on lava substrate, often in moist climates (Smathers and Mueller-Dombois, 1974). This paper reports six years of plant succession on tephra (fine-grained ash and coarser particles of pyroclastic origin) of arid Isla Fernandina, westernmost island of the Galápagos archipelago. These islands are one of the most active volcanic fields on earth, and their biology is closely related to their volcanic history.

In May, 1968, Fernandina, a basaltic shield volcano, experienced a violent summit eruption and caldera collapse (Simkin and Howard, 1970). One feature of this activity was a ground-level surge of tephra from the caldera floor up on to the rim of the caldera and 10 km downslope to the sea. This was a cool, wet, sticky, high density, and high velocity flow (B. Nolf, pers. comm., 1977). Vegetation was obliterated in an area of approximately 25 km² on the western slope of the volcano and variously damaged in an area three times that. A few patches escaped in the lee of topographic shelters. Destruction was by burial under as much as 8 m of tephra toward the center of the flow (B. Nolf, pers. comm., 1977) and by uprooting, breaking, debarking, and partial burial toward the shallower edges.

On the Galápagos Islands lava flows are the major alternative substrate to tephra. Lava flows present a most inhospitable habitat for plant colonization, and most are barren for long periods. For example,

one 1825 flow south of Punta Espinosa, Fernandina (B. Morrell, 1825, cited in Brower, 1968) had almost no plants growing on its surface after 150 years. By contrast, revegetation of the tephra on the rim of Fernandina was easily visible within nine years.

The pre-eruption vegetation on the northeast caldera rim of Fernandina was a dense tangle of shrubs and herbs described qualitatively by Eliasson (1972) and Colinvaux (1968) as 2–3 m tall shrub forest dominated by *Scalesia microcephala* Robins. Similarly, on the northwest section of the rim *Scalesia microcephala* was a dominant shrub, but of nearly equal size and numbers were *Zanthoxylum fagara* (L.) Sarg., *Tournefortia rufo-sericea* Hook. f., and *Solanum erianthum* D. Don. Also present were *Darwiniothamnus tenuifolius* var. *glandulosus* (Harling) Cronq., *Lippia rosmarinifolia* Anderss. var. *rosmarinifolia, Baccharis gnidiifolia* HBK., *Alternanthera filifolia* (Hook. f.) Howell, and a number of smaller shrubs and herbs. This shrub forest still existed apparently undisturbed around half of the rim and was, therefore, available as a source of plants for recolonization of the tephra.

METHODS

Reestablishment of rim vegetation on the tephra was studied 3, 5, and 9 years after the eruption (June, 1971; July, 1973; and August, 1977). A transect was established beginning on deep tephra at a permanent metal post marking the high point (1494 m) of the west rim and running 18° east of due north. The transect extended north approximately 1.2 km across deep barren tephra (Fig. 1) and continued ¼ km across sparsely vegetated shallow tephra (Fig. 2) to the boundary of the original forest. In the barren area a circular plot of 9.1 m radius was established every 91 m and a count made of all plants encountered. In the sparsely vegetated area, circular plots of 1.5 m radius were established every 15 m for count of herbaceous species; in addition, a plot of 9.1 m radius was established at each third site (46 m intervals) for a count of shrub species. The same plots were resampled each year of the study, except that in 1977 the solitary 1.5 m radius plots were omitted.

In 1973 additional sampling was done (3.1 m radius circular plots at 91 m intervals) along a ⅓ km line extending south from the southern edge of the barren tephra.

In 1977 land iguana (*Conolophus* sp.) feces found in the plots were collected and the seeds they contained brought back to the laboratory. The seeds were tested for germination ability to determine if iguanas provide a possible means of seed dispersal to and across the tephra. Samples from 11 sites along the transect were put on moist paper in petri plates and placed in light.

Fig. 1.   View north from about meter 500 of the rim transect, 1977. Here the tephra layer was deep enough to destroy the vegetation entirely. Gullies interrupt the hard, smooth surface evident at the left foreground. Grass clumps visible at right are 0.2–0.3 m tall.

RESULTS

Distribution and density of dominant species encountered along the transect are shown in Fig. 3. The transect crossed three communities— barren, shrub, and the ecotone between them. These are discussed separately below.

Barren area.   Toward the center of the tephra, where the deposit was thickest and the destruction of vegetation complete, little reveg- etation occurred in the nine years following eruption. Approximately 3 km of the rim along the west side of the caldera were still practically barren, another 3 km to the south only sparsely vegetated. The surface of the tephra was a hard crust of fine-grained material, broken in places by gullies centimeters to meters deep exposing coarser textured layers (Fig. 1). Hardening of the surface apparently occurred soon after deposit, as photos taken in successive years show essentially no change in gully pattern or size.

Even the hardiest plants rarely were found growing on the hardened tephra surface. Colonization occurred almost exclusively where the surface was broken. Most plants grew in gullies, in the lines where the wall of the gully met the floor. Here seeds blown from the sur- rounding area could accumulate; the broken surface and occasional shade increased the seedlings' chances of success. A second site of

FIG. 2.   View north along the northern ¼ km of the rim transect, 1971. Here at the tapering edge of the tephra layer, vegetation was only partially destroyed. Most vegetation visible is 0.5–1.5 m tall.
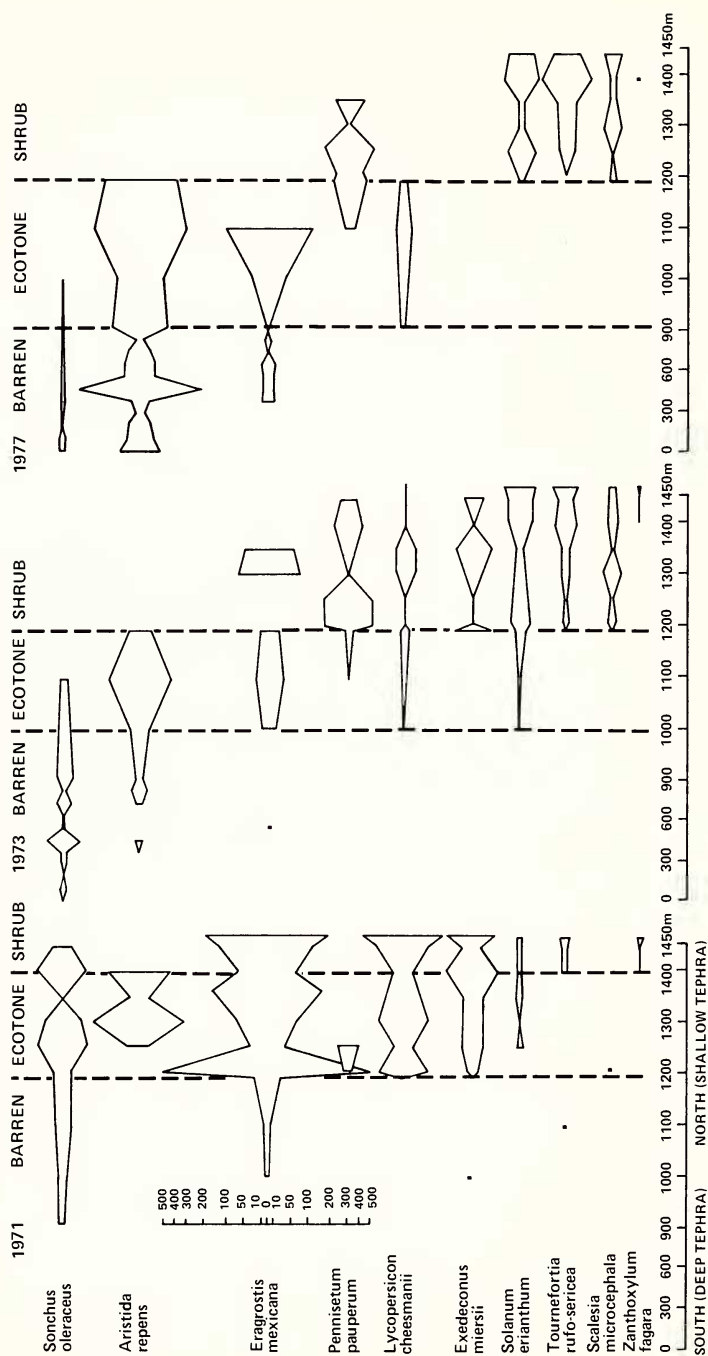
Fig. 3. Distribution and density of dominant species by year. The horizontal axis represents location along transect. Note change of scale at 900 m. The vertical scales represent number of plants per 0.025 ha (log scale).

colonization was at the base of rocks where morning fog condensing on the cool rock face could run to the ground. A third site was provided by scattered depressions that appeared to contain water at some time during the year. In the highlands of Santa Cruz, vegetation is most lush during a cool season from July to December (Van der Werff, 1979). No precipitation records are available for the rim of Fernandina; the few days observed in this study (June, July, and August) were dry. The limiting factors for plant growth on the tephra appeared to be lack of moisture and of appropriate establishment sites.

Few species were able to grow at all in these conditions. Only three were found with any regularity: *Sonchus oleraceus* L., an annual, cosmopolitan, weedy composite; *Aristida repens* Trin., an annual, endemic, weedy grass; and *Eragrostis mexicana* (Hornem.) Link, a widespread, tropical, weedy grass. Other species found less frequently were *Eragrostis ciliaris* (L.) R. Br., *Cyperus ligularis* L., and *Muhlenbergia microsperma* (DC.) Kunth, widespread tropical weedy species, and *Cyperus anderssonii* Boeck. and *Verbena townsendii* Svens, Galápagos endemics. Between 1971 and 1977 these species became less abundant at the north of the transect as shrubs grew and more abundant to the south as gradual breakup of the hard surface occurred (Fig. 3).

Ecotone. This community is defined by the scarcity of any shrubs except *Solanum erianthum* and *Baccharis gnidiifolia* and the presence of three herbaceous species not found in the "barren" community: *Pennisetum pauperum* Steud. is a large perennial grass, endemic to Fernandina and Isabela high-elevation lava and cinder beds. *Lycopersicon cheesmanii* Riley, a short-lived perennial endemic to the Galápagos, and *Exedeconus miersii* (Hook. f.) D'Arcy, an annual common in the Galápagos at sea level on sandy substrata and found also in Peru, are sprawling vines of the Solanaceae. All three are found only sparsely in the undisturbed original forest but are highly successful pioneer species on the edge of the tephra. No *Exedeconus* was found anywhere at the rim in 1977. The moisture-retaining surface layer of tangled vegetation and litter resulting from growth of these species provides a habitat in which other plants can grow.

In 1977 the tiny moss *Bryum argenteum* Hedw. was found growing in extensive patches in this area. The capsules are only 8–9 mm high, and in August the entire plant appeared simply as a darker crust on the hard tephra surface. Interestingly, this species was also a post-eruption pioneer on the island of Surtsey in the North Atlantic (Fridriksson, 1975).

In 1971 much of the northern ¼ km of the transect could be defined as "ecotone." In 1973 and 1977 the ecotone community was a distinct band moving onto the tephra. This band was about 180 m wide in 1973 and 270 m wide in 1977. Figure 3 indicates the sharp demarcation

of the advancing edge of vegetation that was evident in the field. This edge between "barren" and "ecotone" communities was defined by the sharp increase in both vegetative cover and number of species. The total number of species encountered in summed samples north of the barren/ecotone line (all "ecotone" plus all "shrub") was 17–19 each year, contrasted with 8–9 species to the south ("barren" samples). This edge advanced approximately 180 m south onto the tephra between 1971 and 1973 and an additional 90 m between 1973 and 1977.

Shrub area.   In contrast to the still barren area at the center of the tephra, the ¼ km at the northernmost edge experienced vigorous revegetation in the nine years following the eruption. Here tephra deposits were thinner and destruction of vegetation less complete than in the km sampled across the barren tephra to the south. A sparse cover of scattered shrubs and herbs in 1971 grew by 1977 to a nearly-impenetrable tangle 2–4 m tall (Figs. 4 and 5). Densities of shrub species by year are given in Table 1.

The major shrub species found in the shrub area were the same that dominated the undisturbed forest to the north, where four species were about equally dense and dominant. During revegetation, however, these four were present in strikingly different proportions. In 1977, *Solanum erianthum* and *Tournefortia rufo-sericea* were twice as numerous as *Scalesia microcephala*. Excavations showed that these two species, especially *Tournefortia rufo-sericea,* were sending up abundant vegetative shoots. Nevertheless, each apparently separate plant that arose without evident aboveground connection to another was counted as an individual. Thus much of the apparent increase in numbers of *Solanum erianthum* and *Tournefortia rufo-sericea* was from a few genets that survived burial under tephra and sprouted vegetatively. In *Solanum erianthum* reproduction by seed also appeared to be vigorous, and it was the only shrub found as occasional pioneer individuals on the deeper tephra.

Scalesia microcephala apparently reproduced by seed only, and individuals of all sizes were present in 1973. By 1977, the majority of *Scalesia* were 2–3 m tall.

Zanthoxylum fagara, common in the original forest, was practically nonexistent in the disturbed area. Nowhere were any small *Zanthoxylum* seen. It appears that new plants become established with difficulty in this habitat but, once established at a later seral stage, persist, as *Zanthoxylum* was well represented in the original forest.

Seed germinability.   Seeds collected from iguana droppings in August, 1977, were tested for germination in December, 1977. In eight of 11 petri plates of seeds, including half of those from the most barren area, seeds germinated after two weeks (22 dicot seeds of at least two species and four grass seeds of two species). None survived long enough for identification.

FIG. 4.   (Upper) view north along the northern ¼ km of the rim transect, 1973. Most shrubs are 1 to 2 m tall.

FIG. 5.   (Lower) view north along the northern ¼ km of the rim transect, 1977. Shrubs are a solid cover 2 to 4 m tall. Compare with Figs. 2 and 4, the same view in 1971 and 1973

TABLE 1. SHRUB DENSITY AVERAGED OVER NORTHERN ¼ KM OF TRANSECT, AREA OF RAPID REVEGETATION ("SHRUB AREA"). Numbers are individuals per 0.1 ha.

	1971	1973	1977
Solanum erianthum	3.8	107	121
Tournefortia rufo-sericea	4.9	52	130
Scalesia microcephala	1.0	41	60
Total shrub density	8.7	200	311

South of barren tephra. Vegetation to the south of the thickest tephra existed in a somewhat different pattern from that at the northern edge. The rim topography to the south was more varied, with more ridges and hollows, and corresponding irregularity in tephra depth and other features of the physical environment. Vegetation here grew not in a distinct advancing front as at the north edge, but in irregular patches. Some of these patches were clearly survivors from the pre-eruption forest; notable were a few sparse stands of *Opuntia insularis* Stewart and several stands of rim shrub forest. In other patches *Solanum erianthum* dominated. Over much of this area grew a sparse grass community, unlike anything to the north. Here grass cover in 1973 ranged from 10–50 percent composed of three species in the following proportions: 4 *Aristida repens* : 2 *Eragrostis mexicana* : 1 *Muhlenbergia microsperma.* Also present were occasional individuals of *Sonchus oleraceus, Cyperus anderssonii, Verbena townsendii, Lycopersicon cheesmanii,* and *Solanum erianthum.*

DISCUSSION

Reproductive strategies. The species found growing on the tephra in the nine years since eruption may be characterized as being to some degree weedy. "Weedy" here denotes possession of some combination of the following characteristics: (1) The plant has the potential for rapid growth in perhaps temporarily favorable conditions and the tolerance to survive harsh environmental conditions. (2) Reproductive potential by seed is high, or, alternatively, ability to grow by root or stem sprouting is well developed. (3) Ability to compete with other plants is poor.

Three reproductive strategies were evident in successful colonizers of the tephra: weedy annuals, rhizomatous perennial herbs, and root-sprouting shrubs.

In the harshest sites of deepest tephra, opportunistic annual herbs were the most effective colonizers. The habitats offering any possibility of success for seedlings were scattered, thus those plants producing a large number of easily dispersed seeds had the greatest chance of successful establishment. Both *Sonchus oleraceus* and *Aristida repens,*

found commonly on the tephra, have fruits with hairs or awns that would facilitate their dispersal by wind across the smooth tephra.

Some species spread after initial establishment by rhizome growth. Although all the grasses on the more barren tephra are cited as annuals by Reeder and Reeder in Wiggins and Porter (1971), my observations suggest that some may behave as perennials. *Eragrostis mexicana* in particular grew in stout-based clumps that appeared to be perennial. Several groups were dug up and found to be connected by rhizomes over a distance of a meter or more. This anomalous behavior is another example of the well-documented plasticity of weed species (Baker, 1965; Mayr, 1965). Because barren tephra is so inhospitable to even the most vigorous colonizers, extensive revegetation must await the slow breakup of the surface.

Vigorous ramet production can be an important mode of growth and monopolization of resources for weedy perennials (Bunting, 1960; Baker, 1965). *Solanum erianthum* and *Tournefortia rufo-sericea,* the two shrub species most successful in early establishment on the tephra, had abundant stem and root sprouting. The apparent predominance of this form of growth in these shrubs helps explain the very rapid revegetation of the edge of the tephra. Shrubs surviving intact and roots or branches shallowly buried may all have sprouted. These shrubs show bursts of increased stem density and size resulting in rapid filling of space. Such a burst made *Solanum* the dominant species by 1973; by 1977 *Tournefortia* had attained equal density (Table 1). This rapid growth is characteristic of early successional stages (Odum, 1969) and frequently accounts for rapid revegetation after volcanic eruption (Sands, 1912; Gates, 1914; Aston, 1916; Griggs, 1918).

Extensive ramet production maintains existing genotypes and present fitness. Its importance in this community supports Pickett's (1976, p. 111) suggestion that "genetic systems favoring reduced recombination are selected for in relatively severe early successional habitats."

Scalesia microcephala showed no evidence of vegetative propagation and was slower to become reestablished. Seedlings were apparently able to compete successfully with earlier shrubs and with each other. Continual recruitment of seedlings (Table 1) suggests that *Scalesia* may eventually regain its original density.

Rate of revegetation.   The rate and pattern of revegetation is influenced not only by differing reproductive and growth strategies but also by rainfall and by land iguanas. The Galápagos are notorious for their year-to-year fluctuations in rainfall. A 12-year record from San Cristóbal (Chatham) Island, for example, shows a range in annual rainfall of 3.6–142 cm (Palmer and Pyle, 1966). It is considerably drier on Fernandina than on San Cristóbal, but fluctuations are extreme here as well. Although no precipitation data are available for the rim

of Fernandina, Boersma (1977), working at Punta Espinosa on the northeast corner of the island, observed no precipitation during June and August, 1971, but frequent cloud cover and precipitation more than 15 times between June and August, 1972. The weed strategies of the rim flora are those to be expected in a harsh and fluctuating environment. Climatic variation over the coming years will play a major role in determining the rate at which revegetation of the tephra will continue.

Land iguanas, found throughout the area, may facilitate revegetation in two ways. They appear to play a role in seed disperal to and across the tephra, as they and their often seed-filled droppings were found on even the most barren areas. They also may influence soil development. Their droppings consists of plant material in various stages of decomposition and during the wet season may provide an excellent germination site for seeds contained within or blown to the droppings. Several workers have suggested that such addition of organic matter, particularly nitrogen, to volcanic tephra is prerequisite to revegetation (Griggs, 1933; Eggler, 1963). In addition, extensive iguana tunnels help break up the solid surface of the tephra. A number of collapsed burrows were observed in the barren and ecotone areas. Plants were growing in each, usually in marked contrast to the surrounding unbroken and barren surface.

Vulcanism and plant communities.   Persistence of the shrub forest on the rim of Fernandina must be considered in the long-term context of volcanic activity. In the western Galápagos there have been at least 29 eruptions in the last 50 years, 40 eruptions in the last 150 years, and 50 eruptions since the first known eruption 183 years ago in 1797 (T. Simkin, pers. comm., 1981). Periodic disturbances must always have been a feature of Fernandina's environment. Indeed, if "vulcanism" is substituted for "competition", Hutchinson's (1951, p. 575) definition of fugitive species seems a singularly apt description of Fernandina's shrub forest: "They are forever on the move, always becoming extinct in one locality as they succumb to competition and always surviving by reestablishing themselves in some other locality as a new niche opens. The temporary opening of a niche need not involve a full formal successional process." One trend usually expected in succession is an increase in species number (Odum, 1969). This was not true of the first nine years of rim revegetation on Fernandina. There was, instead, rapid recolonization by most of the same few species found in the original climax forest. Whittaker (1965, p. 257) pointed out that "severe, unstable, and recent environments limit the numbers of species which have evolved to maintain themselves in these environments." Earlier workers on Fernandina tephra (Colinvaux et al., 1968; Eliasson, 1972) reported species not represented in these samples; these may well become established here in the future.

Revegetation of the Fernandina tephra supports Porter's (1976, 1979) description of the Galápagos flora as basically weedy. In this arid and periodically disturbed environment, it appears that selection has been for weedy species able to enter new terrain quickly and persist in or at the edges of mature shrub communities. Root and stem sprouting by shrubs is one means of maintaining populations in the face of periodic moderate disturbance. Classic herbaceous weed strategies predominate in areas of the most serious disturbance. Thus in the unstable environment of this active volcano, communities are composed of variously resilient species able to recover from disturbance and revegetate newly created open habitats.

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